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# REVISION OF *OPHIOPAEPALE* LJUNGMAN, 1872 (ECHINODERMATA: OPHIUROIDEA), WITH A REDESCRIPTION OF *O. GOESIANA* LJUNGMAN, 1872, AND NOTES ON *O. DIPLAX* (NIELSEN, 1932), NEW COMBINATION

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*Abstract.*—*Ophiopaepale* Ljungman, 1872, is revised. *Schizoderma* Nielsen, 1932, is a junior synonym. *Ophiopaepale* now includes two species, which form a geminate pair from tropical American waters: *O. goesiana* Ljungman, 1872, type-species, West Indies and Gulf of Mexico, redescribed herein; *O. diplax* (Nielsen, 1932), n. comb., type-species of *Schizoderma,* Gulf of Panama and other eastern tropical Pacific localities. Synonymy was required by the discovery of fragmented dorsal arm plates in *O. goesiana* and the presence of tables comprising the disc granulation of both species. *Ophiopaepale* is distinguished from other ophiuroid genera by the division of each ventral arm plate into proximal and distal halves.

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Nielsen (1932) erected *Schizoderma* as a new monotypic genus of ophiodermatid brittle star from the Gulf of Panama. He distinguished it from the closely related, monotypic, West Indian genus *Ophiopaepale* Ljungman, 1872,[1] by the presence in *Schizoderma* of fragmented dorsal arm plates and dorsally elongated genital slits. Nielsen was aware of the geologic history of the Isthmus of Panama and its role in formation of geminate species (1932:245); it is, therefore, surprising that he did not more closely examine the holotype of *O. goesiana* Ljungman, 1872, for comparison with his new material. Since Nielsen's (1932) original description, there has only been brief mention of *Schizoderma* by Clark (1940), Fell (1960), and Spencer and Wright (1966). Examination by the present author of recently collected *O. goesiana* from the southwest Florida shelf revealed the presence of fragmented dorsal arm plates along most of the arm length. This condition has been confirmed in the holotype. Based on this observation, an amended diagnosis of *Ophiopaepale* is given, *Schizoderma* is relegated to synonymy, and *O. goesiana* is redescribed.

## Family Ophiodermatidae Ljungman, 1867

### *Ophiopaepale* Ljungman, 1872

*Ophiopaepale* Ljungman, 1872:615–616 (diagnosed), 639 (key).—Lyman, 1882: 17–18 (diagnosed).—Nutting, 1895:78 (listed).—Bather et al., 1900:278 (listed

[1] This work is mistakenly dated 1871 by most authors who credit Ljungman with the several new genera, species, and varieties described therein. The error arises from the fact that the work was published (in 1872) in a volume which reported Proceedings of the Academy for 1871.

in systematic review as *Ophiopaepale* Lym.).—Meissner, 1901:906, 909, 912 (listed in systematic review), 919 (diagnosed).—Delage & Hérouard, 1903:150 (diagnosed).—Clark, 1915:346 (listed).—Matsumoto, 1915:83 (listed in systematic review).—Clark, 1921:34 (zoogeographic list).—Nielsen, 1932:338–339 (compared to *Schizoderma*).—Fell, 1960:27 (key).—Spencer & Wright, 1966: 98 (listed in systematic review).—Madsen, 1983:30 (listed).

*Schizoderma* Nielsen, 1932:243 (listed), 327 (key), 335 (diagnosed), 338–339 (compared to *Ophiopaepale*) (type-species, *Schizoderma diplax* Nielsen, by monotypy).—Fell, 1960:27 (key).—Spencer & Wright, 1966:98 (listed in systematic review).

*Diagnosis.*—Disc arcuate pentagonal; abactinal surface flat or sunken; granulated with tables on both surfaces. Radial shields connected interradially by a few large marginal plates. In each interradius, 1 pair of long genital slits extending at least to edge of disc and visible when viewed from above. Arms long, slender, with 3–4 arm spines. Dorsal arm plates fragmented; ventral arm plates divided transversely into proximal and distal halves. 1 tentacle scale.

*Type-species.*—*Ophiopaepale goesiana* Ljungman, 1872, by monotypy.

*Remarks.*—*Ophiopaepale,* as redefined herein, includes two species. In addition to features described by Nielsen (1932), both species have fragmented dorsal arm plates, and the disc granulation consists of tables. Each table consists of a base and spire (Fig. 1A, B) but is larger and morphologically more complex than that of aspidochirote holothuroids. Species-specific differences in table morphology have not yet been found in *Ophiopaepale,* but they differ from the non-tabular granules of *Ophioderma* (Fig. 1C, D). The species differ in number of marginal disc plates, length of genital slits and arrangement of associated ossicles, granulation of the oral frame, relative length of arms and vertebrae (Fig. 2A, B; cf. *Ophioderma,* Fig. 2C), fragmentation pattern of dorsal arm plates, morphology of tentacle scales, and length of arm spines.

### *Ophiopaepale goesiana* Ljungman, 1872
Figs. 1A, 2A, 3A–E, 4A–C, 5A–E

*Ophiopaepale goesiana* Ljungman, 1872:615–617 (diagnosed and described), 650 (zoogeographic list).—Lyman, 1875:3 (listed); 1878:228 (material); 1882:18, 313, 315 (listed), pl. 37, figs. 4–6; 1883:228 (listed), 233 (material, part).—Agassiz, 1888:111 (listed), fig. 393.—Nutting, 1895:81 (briefly described).—Verrill, 1899a:8 (material); 1899b:373 (listed).—Meissner, 1901:919 (listed).—Koehler, 1904:54 (listed), 57–59 (redescribed), figs. 1–4; 1907:287 (listed); 1914: 48 (material).—Clark, 1915:346 (material).—Clark, 1921:44–50 (zoogeographic & station lists).—Nielsen, 1932:338–339 (compared to *Schizoderma diplax*).—Clark, 1941:106 (material), 139 (station list).—Clark, 1954:378 (zoogeographic list).—Fell, 1960:27 (listed).—Spencer & Wright, 1966:98 (listed).

Non *Ophiopaepale goesiana* Lyman, 1883:233 [part; (MCZ 797), 1 dry specimen, disc diameter 1.0 mm, *Blake* sta 127, is a young *Ophiomusium* or *Ophiosphalma*].

*Material.*—HOLOTYPE (Naturhistoriska Riksmuseet Stockholm 1447): alcoholic specimen, disc diameter (dd) 5.7 mm; Anguilla; 1870, 180 fm.

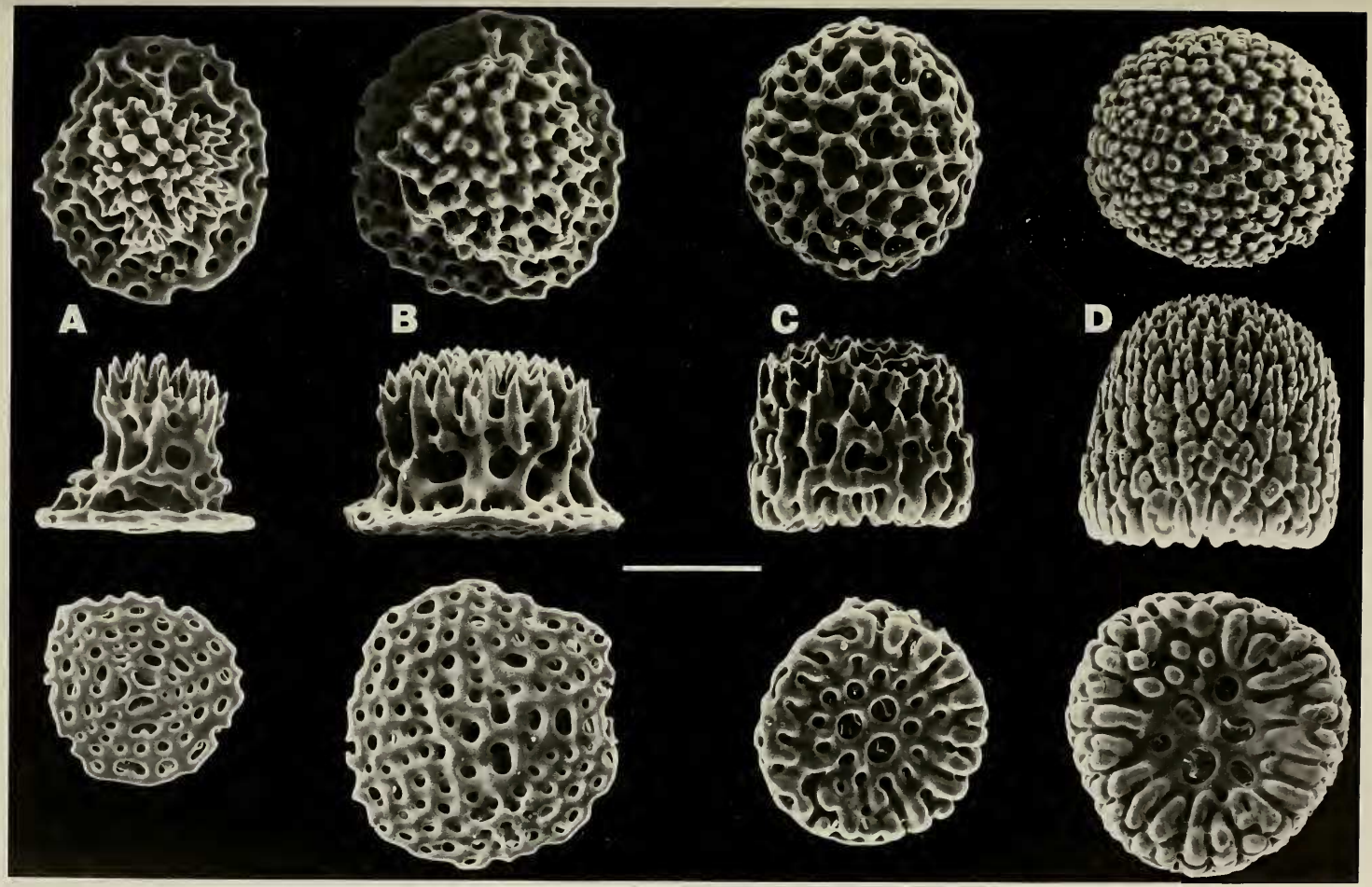



Fig. 1. Disc granules: apical (top row), side (middle row), and basal (bottom row) views. A, *Ophiopaepale goesiana,* USNM E30826; B, *Ophiopaepale diplax,* MCZ 5459; C, *Ophioderma cinereum,* Carrie Bow Cay, Belize; D, *Ophioderma appressum,* Carrie Bow Cay, Belize. Scale bar, 0.05 mm.

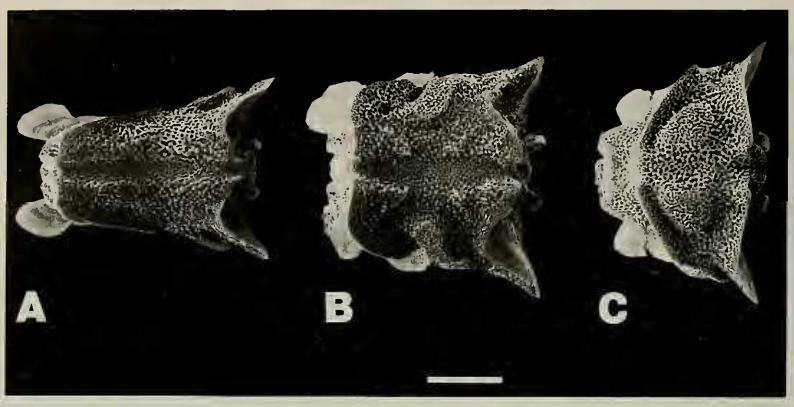



Fig. 2. Vertebrae from base of arm, near disc, abactinal views. A, *Ophiopaepale goesiana,* Holotype; B, *Ophiopaepale diplax,* MCZ 5459; C, *Ophioderma cinereum,* Carrie Bow Cay, Belize. Scale bar, 0.5 mm.

Non-type material: (MCZ 248), 1 dry spec., dd 10.4 mm; off Barbados; *Blake,* sta 272 and/or 297, 1878–1879, 76 fm and/or 123 fm.—(MCZ 249), 1 dry spec., dd 5.1 mm; Gulf of Mexico; *Blake,* sta 45, 1877–1878, 25°33′N, 84°21′W, 101 fm.—(MCZ 250), 1 dry spec., dd not measurable; off St. Vincent; *Blake,* sta 269, 1878–1879, 124 fm.—(MCZ 251), 1 dry spec., dd 5.8 mm; off Barbados; *Hassler* Expedition, 100 fm.—(MCZ 253), 2 dry spec., dd 6.5, 9.5 mm; off Grenada; *Blake,* sta 253, 1878–1879, 92 fm.—(MCZ 793), 2 alcoholic spec., dd 4.3, 5.4 mm; off Montserrat; *Blake,* sta 155, 1878–1879, 88 fm.—(MCZ 794), 3 alcoholic spec., dd 7.6–10.4 mm; off Havana; *Blake,* 1877–1878, 80–242 fm.—(MCZ 795), 3 alcoholic spec., dd 5.5–7.3 mm; same data as MCZ 250.—(MCZ 796), 1 alcoholic spec., dd 9.8 mm; St. Cruz, off Frederickstadt; *Blake,* sta 132, 1878–1879, 115 fm.—(MCZ 962), 1 dry spec., dd 7.7 mm; same data as MCZ 793.—(MCZ 6552), 1 dry spec., dd 8.1 mm; Old Bahama Channel, off Cayo Coco, Camaguey Province; Harvard-Havana Expedition, *Atlantis,* sta 3400, 28 Apr 1939, 180 fm.—(USNM 6491), 2 alcoholic spec., dd 5.7, 6.5 mm; off Barbados; *Blake,* sta 293, 1878–1879, 82 fm.—(USNM 7176), 3 alcoholic spec., dd 6.3–8.7 mm; *Albatross,* sta 2163, 30 Apr 1884, 23°10′31″N, 82°20′29″W, 133 fm.—(USNM 10184), 1 alcoholic spec., dd 6.9 mm; *Albatross,* sta 2319, 17 Jan 1885, 23°10′37″N, 82°20′06″W, 143 fm.—(USNM 10187), 1 dry spec., dd 5.2 mm; off Havana; *Albatross,* sta 2329, 17 Jan 1885, 23°11′03″N, 82°18′45″W, 118 fm.—(USNM 12396), 5 dry spec., dd 6.4–9.9 mm; *Albatross,* sta 2327, 17 Jan 1885, 23°11′45″N, 82°17′54″W, 182 fm.—(USNM 12411), 7 alcoholic spec., dd 6.2–9.8 mm; *Albatross,* sta 2159, 30 Apr 1884, 23°10′39″N, 82°20′08″W, 98 fm.—(USNM 12487), 1 dry spec., dd 6.7 mm; off Havana; *Albatross,* sta 2166, 1 May 1884, 23°10′36″N, 82°20′30″W, 196 fm.—(USNM 12506), 1 dry spec., dd 8.6 mm; off Havana; *Albatross,* sta 2160, 30 Apr 1884, 23°10′31″N, 82°20′37″W, 167 fm.—(USNM 12513), 1 dry spec., dd 9.9 mm; off Havana; *Albatross,* sta 2161, 30 Apr 1884, 23°10′36″N, 82°20′28″W, 146 fm.—(USNM 15286), 5 alcoholic spec., dd 7.7–10.1 mm; *Albatross,* sta 2322, 17 Jan 1885, 23°10′54″N, 82°17′45″W, 115 fm.—(USNM 15290), 3 alcoholic spec., dd 6.3–10.2 mm; *Albatross,* sta 2348, 20 Jan 1885, 23°10′39″N, 82°20′21″W, 211 fm.—(USNM 15306), 2 alcoholic spec., dd

6.7, 7.4 mm; *Albatross,* sta 2337, 19 Jan 1885, 23°10′39″N, 82°20′21″W, 199 fm.—(USNM 15312), 6 alcoholic spec., dd 9.0–10.2 mm; *Albatross,* sta 2336, 19 Jan 1885, 23°10′48″N, 82°18′52″W, 157 fm.—(USNM 15350), 3 dry spec., dd 7.6–9.4 mm; *Albatross,* sta 2320, 17 Jan 1885, 23°10′39″N, 82°18′48″W, 130 fm.—(USNM 15394), 1 dry spec., dd 10.2 mm; off Havana; *Albatross,* sta 2346, 20 Jan 1885, 23°10′39″N, 82°20′21″W, 200 fm.—(USNM E3663), 1 dry spec., dd 9.4 mm; off Puerto Rico; Johnson Smithsonian Expedition, sta 679, 1933.—(USNM E4294), 5 alcoholic spec., dd 7.8–10.4 mm (2 not measurable); off Havana, Morro Castle, bearing SW by W, about 2½ mi; Bahamas Expedition, sta 2, 24 May 1893, 110 fm.—(USNM E6302), 5 dry spec., dd 7.2–9.8 mm; Havana; State University of Iowa Biological Expedition to the Florida Keys and the West Indies, sta 2.—(USNM E11852), 1 dry spec., dd 7.7 mm; *Oregon,* sta 5624, 25 Sep 1965, 10°52′N, 66°08′W, 56 fm.—(USNM E28509), 3 alcoholic spec., dd 9.6–10.9 mm; Little Bahama Bank; *Gerda,* sta 251, 5 Feb 1964, 27°25′N, 78°41′00″W to 78°37′30″W, 293–311 m.—(USNM E30823), 1 alcoholic spec., dd 7.7 mm; Gulf of Mexico; U.S. Bureau of Land Management, Southwest Florida Shelf Ecosystems Study, Year 2, Cruise II (BLM 321-II), sta 35, 26 Jul 1981, 25°44.8′N, 84°21.0′W, 159 m, otter trawl.—(USNM E30824), 2 dry spec., dd 5.3, 6.6 mm; same data as USNM E30823, triangle dredge.—(USNM E30825), 2 dry spec., dd 10.4, 11.1 mm; Gulf of Mexico; BLM 321-II, sta 36, 2 Aug 1981, 25°16.8′N, 83°57.4′W, 127 m, otter trawl.—(USNM E30826), 1 alcoholic spec., dd 10.4 mm; same data as USNM E30825, triangle dredge.—(USNM E30827), 1 dry spec., dd 10.0 mm; Gulf of Mexico; BLM 321-III, sta 32, 6 Feb 1982, 26°16.7′N, 84°04.1′W, 137 m, otter trawl.—(USNM E30828), 1 alcoholic spec., dd 9.3 mm; same data as USNM E30827, triangle dredge.

*Diagnosis.*—3 plates at margin of disc in each interradius; middle plate wider than long. Genital slit extending to edge of disc; not bordered by specialized papillae and scales. Oral shields cordiform, naked centrally. Arm length 8–10 times disc diameter. Dorsal arm plates moderately fragmented; distal border composed of 2–4 subequal pieces. Distal tentacle scales spiniform.

*Morphology.*—The disc is arcuate pentagonal and firmly fused to the 5 arms. Strongly calcified margins of the disc support the thin integument of the central abactinal and interradial actinal surfaces. Dense granulation covers all abactinal and most actinal disc plates. The sunken abactinal integument consists of crowded, imbricating, polygonal scales, which are smaller near the center of the disc and increase gradually in size toward the disc margin; the largest scales are between the paired radial shields (Fig. 3C). The diameter of the disc granules changes similarly. The radial shields are large, convex, smooth, broadly rounded and thick distally, becoming thin and more scale-like proximally; the adradial margins of members of a pair are divergent and extend proximally as inward processes as illustrated by Lyman (1882); a similar but shorter process occurs at the proximal end of the abradial margin of each radial shield. Interradially, 3 large ossicles in series give a prominent margin to the disc (Fig. 3C). The middle ossicle is trapezoidal to rectangular, with its longer side parallel to the disc margin; it overlaps at each end another shorter ossicle which in turn overlaps the radial shield. Although the marginal ossicles and radial shields are obscured by granulation, the tumid condition of these plates gives the disc margin a lumpy appearance that reveals their location.

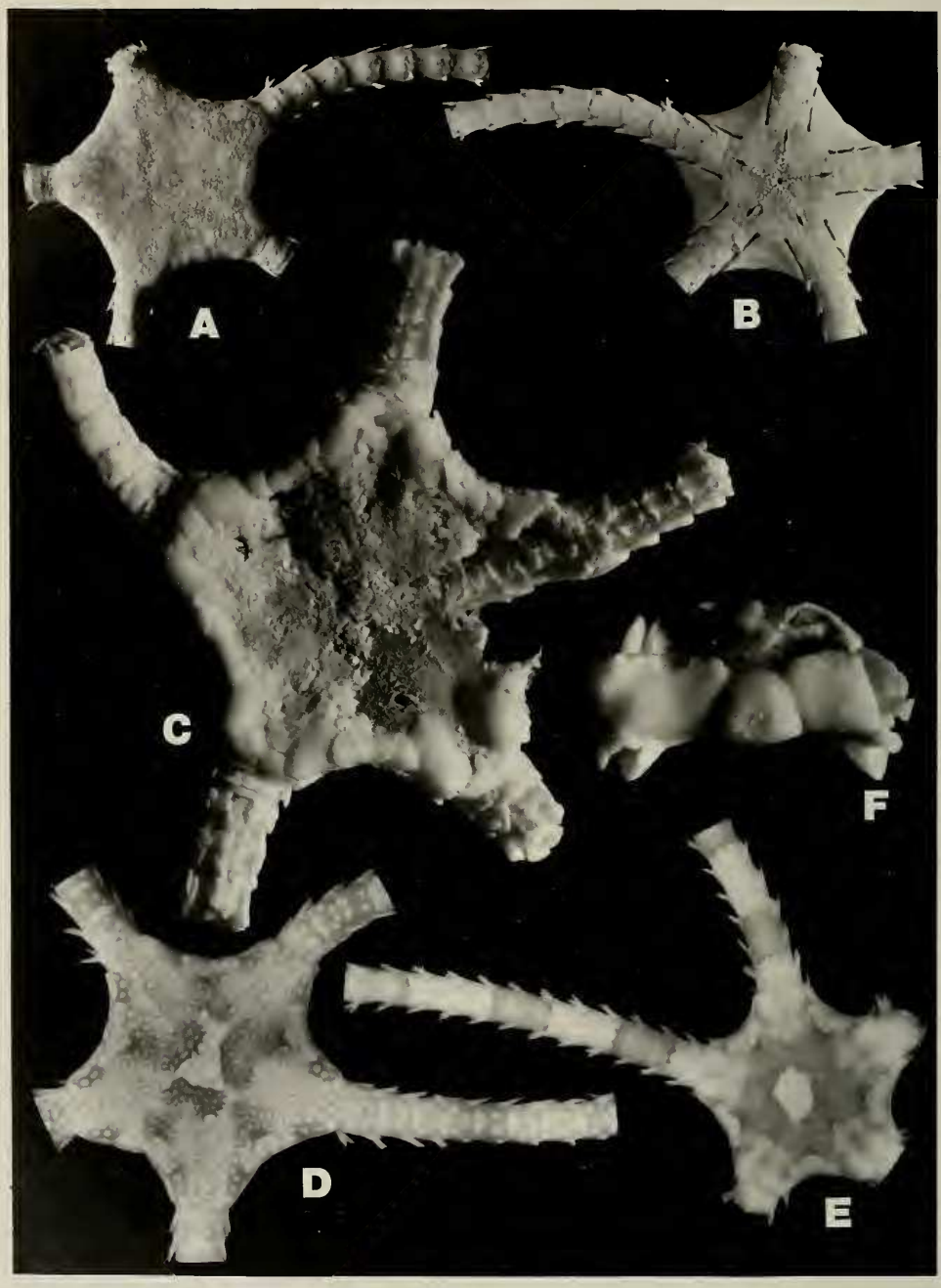
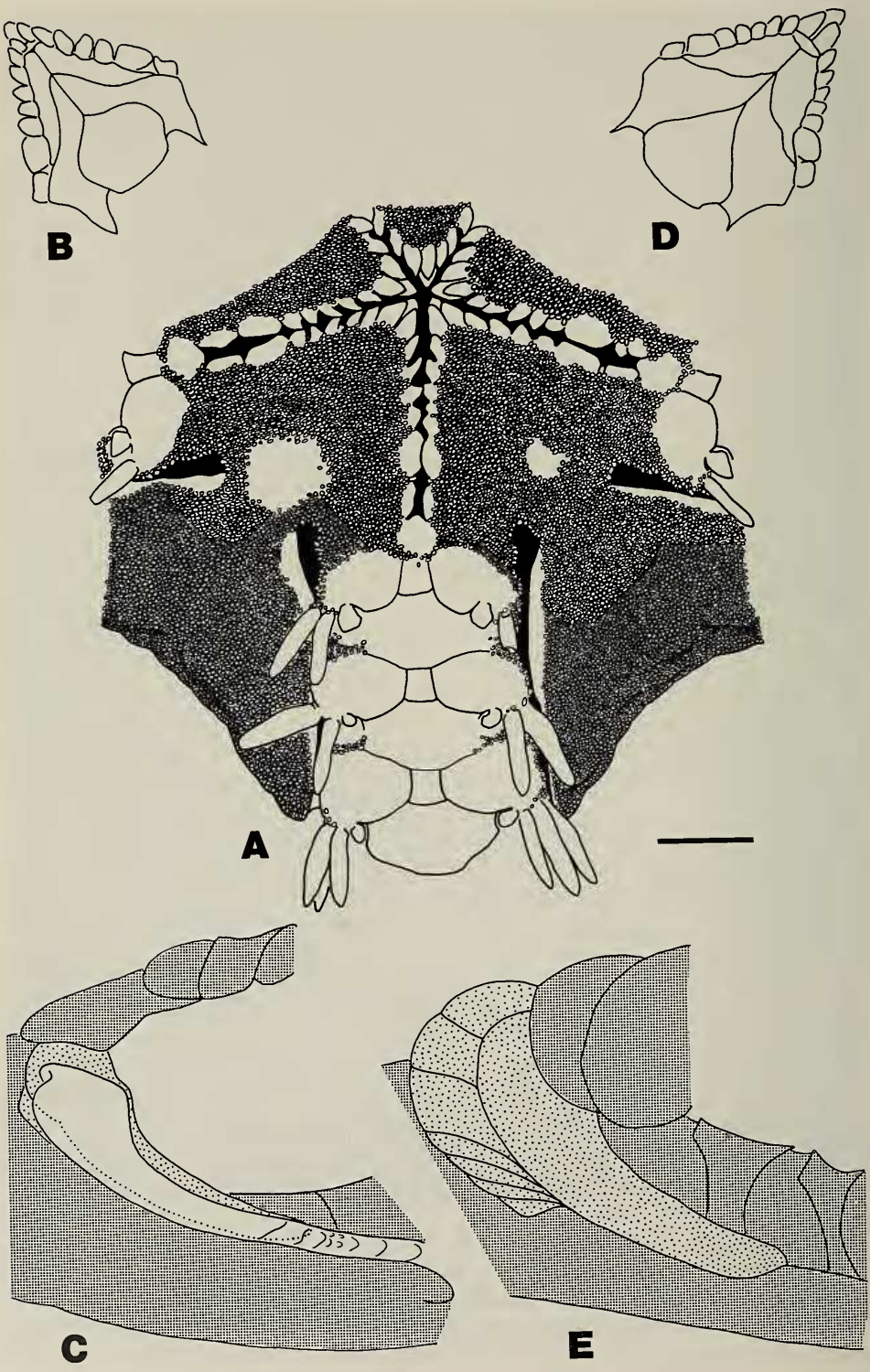



Fig. 3. General morphology and color patterns. *Ophiopaepale goesiana*: A, Abactinal view, Holotype, disc diameter 5.7 mm; B, Same, actinal view; C, Abactinal surface, partly digested with alkali, USNM E30825, disc diameter 11.1 mm; D, Abactinal view, USNM 12411; E, Same, USNM 6491, disc diameter 6.5 mm. *Ophiopaepale diplax*: F, Abactinal view of an interradius digested with alkali, showing interradial plate, radial shields, and associated genital bar and scales, MCZ 5459, disc diameter 13.8 mm.

The central actinal surface is flat and sharply demarcated from the steeply sloping, triangular, concave interradial surfaces. Most of the oral frame, including the bottom edge of the dental plate, is densely granulated, and the shapes and orientation of the major ossicles are not visible without removal of the granules. Only the central part of the oral shield is naked. There are 3–5 robust, symmetrical, lanceolate teeth borne in a vertical row, each tooth usually on a separate piece of the fragmented dental plate. In addition, the lowest piece bears a pair of smaller, asymmetrical, lanceolate teeth of equal or unequal size; if equal, they are aligned horizontally and are a pair of "infradental papillae"; if unequal, they are aligned vertically or obliquely, the smaller lying beneath the larger, giving the impression of an unpaired "infradental papilla"; in some cases, a third tooth is present on the lowest piece of the dental plate. Tooth papillae are absent. There are 6–8 oral papillae (5–7 on the holotype), the distalmost borne on the adoral shield and the others on the oral plate. The proximal oral papillae are asymmetrical, lanceolate, and point obliquely toward the center of the actinal surface; they are more spiniform and longer nearer the jaw apex and more lamelliform distally. The distalmost 2 oral papillae are rectangular, lamelliform; the next to last is the largest oral papilla, longer than wide (almost 3:1 in the holotype), and closing the oral gap; the distalmost is somewhat smaller, longer than wide, often with a concave adradial edge and not closing the oral gap. An additional oral papilla or enlarged granule sometimes lies between the 2 rectangular papillae. The oral plates are elongate triangles, with the shortest sides of a pair in contact abradially (Fig. 4B); the other 2 sides of each plate taper to an apex near the junction of the 2 distalmost oral papillae. The adoral shields join in front of the oral shield and extend to the first ventral and lateral arm plates of adjacent arms; the proximal and distal margins, formed by contact with the oral plate and oral shield, respectively, are somewhat parallel. The oral shield is cordiform. On the interradial actinal surface, dense granulation covers small, thin, imbricating scales, through which the gonads can be seen when the granulation is removed from alcoholic specimens. The granulation extends onto the genital scales and ends at the edge of the genital slit. In each interradius there are 2 genital slits, each of which extends from the adoral shield to the edge of the disc, where the broadened, distalmost genital scale and the genital bar meet and form a specialized groove (Fig. 4C; see also Lyman 1882, pl. 37, fig. 4). The end of the groove can be seen in abactinal view, but it does not appear to curve upward onto the abactinal surface. No specialized granules, papillae, or scales occur along the genital slits.

The arms are long (8–10 times the disc diameter), slender, and taper uniformly to acute tips. The arms are usually widest at segment 3 (rarely segment 4; segment 2 on the holotype). Arm segments are wider than long (5:3 in larger specimens, 6:5 in smaller ones on the fourth free segment from the disc), but the vertebrae are longer than wide (Fig. 2A; see also Lyman 1882, pl. 37, figs. 5, 6). The segments are about as high as wide proximally, but distally the arms are flattened. Each segment is swollen distally because the lateral arm plates angle outward and the dorsal arm plate bulges upward just before the distal margin (Fig. 5A, C); this arrangement gives a beaded appearance to the arm, especially in smaller specimens and on the distal part of the arm. All dorsal arm plates are fragmented, strongly convex, and trapezoidal, with the distal margin wider. The distal margin is straight


B
D
A
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E

or somewhat undulating and composed of 2–4 rectangular pieces, wider than long. The lateral margin is straight and composed of 2–3 additional rectangular pieces. Centrally there are a few pieces of variable shape. Typically, the dorsal arm plate consists of 9 pieces in 3 rows of 3 pieces each, all closely fitted as if made of fused porcelain tiles (Fig. 5C). The junctions of adjacent pieces are difficult to see without treatment with alkali and careful illumination. Each lateral arm plate bears rows and columns of many fine glassy tubercles on its surface. The first ventral arm plate is hexagonal, wider than long, and undivided. The remaining ventral arm plates are divided into two pieces: a short proximal piece lying between the lateral arm plates of a given segment; a wide distal piece lying between the paired lateral arm plates of two adjacent segments. The proximal piece is square or subrectangular on basal segments, with a convex distal margin and straight or slightly convex lateral margins; on distal segments, the proximal piece becomes very elongate with strongly convex lateral margins (Fig. 5E). The distal piece is somewhat octagonal; the distal margin is straight or slightly concave centrally, where it meets the proximal piece of the next segment, and enters a convex curve distolaterally, where it meets the lateral arm plates of the next segment; the distolateral margins curve sharply into the nearly parallel lateral margins, ending at the tentacle pores; the proximal margin is strongly concave at the lateral arm plates and less concave at its junction with the proximal piece. On distal segments, the distal piece becomes more semicircular or sometimes bilobed. Proximal ventral arm plates lack paired pores characteristic of some other ophiodermatid species. There are 3 arm spines, usually appressed and pointing slightly upward. Segment 1 usually bears 2 (rarely 1) spines on each side; segment 2 usually 2–3 spines; segment 3 almost always 3 spines. On the distal half of the arm, 4 arm spines are sometimes present. Arm spines are straight, subconical, subacute, becoming more flattened and acute on distal segments. The upper 2–3 arm spines of distal segments typically have dentate upper edges (Fig. 5B). The upper arm spine of basal segments is robust, ½ to 1 times the segment length; those on the rest of the arm are about ½ the segment length; the middle arm spine is smaller, and the lower arm spine is the smallest. Tentacle scales are single. Tentacle scales of the basal arm segments are lamelliform, oval, lanceolate, or trapezoidal, with the point of attachment to the lateral arm plate narrower than the maximal width. Scales of distal segments are progressively more spiniform and are morphologically similar to, but flatter than, the arm spines (cf., Figs. 4A and 5E). Tentacle scales are ⅓ to ½ the length of the lower arm spine. Granulation extends onto the base of the arm. Abactinally, the first free arm segment is heavily covered with granules, although most of the surface of the distal row of fragments is bare, as is occasionally the surface of more proximal fragments; the granulation extends onto the lateral arm plates.

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Fig. 4. *Ophiopaepale goesiana*: A, Actinal view of granulated specimen, USNM E30827; B, Oral frame, granules removed, MCZ 795; C, Side view of arm with interradial integument removed to show orientation of genital ossicles; genital bar and an accessory scale (light stipple); genital scale (white); base of arm, radial shield, and interradial plates (heavy stipple); USNM E30825. *Ophiopaepale diplax*: D, Oral frame, granules removed, MCZ 6173; E, Same view as C with genital scale removed, MCZ 5459. Scale bar, 1 mm.

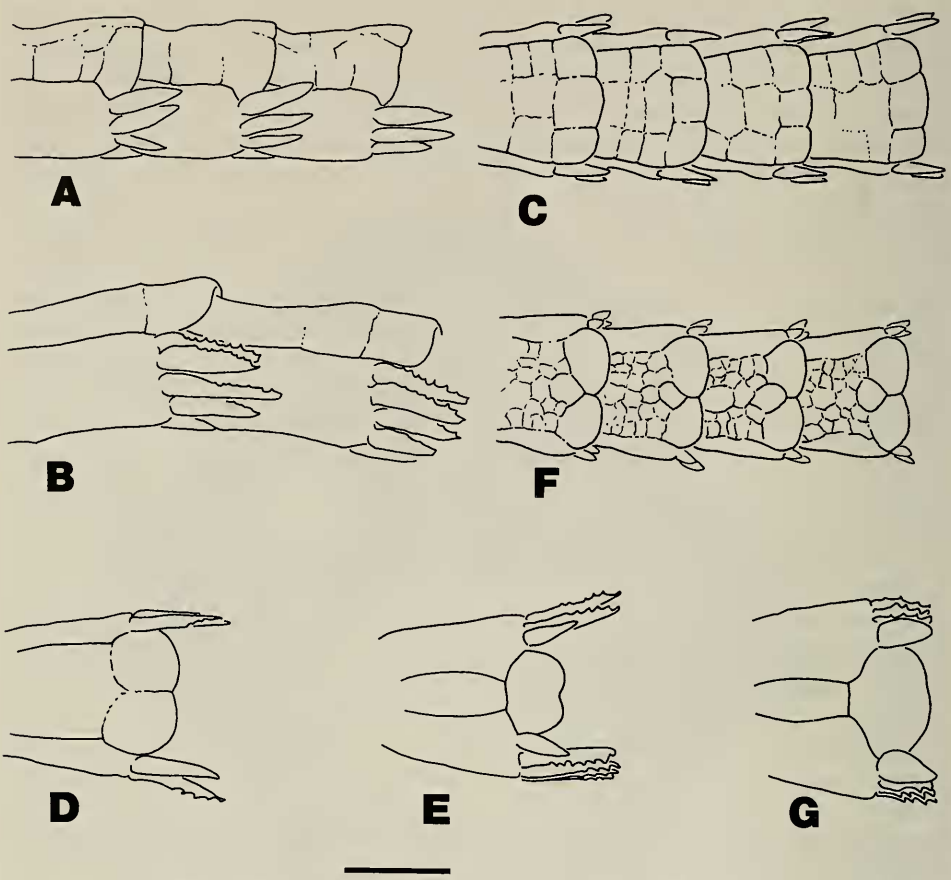


Fig. 5. *Ophiopaepale goesiana*: A, Side view of proximal arm segments, USNM E6302; B, Same, distal arm segments, USNM 15394; C, Abactinal view of proximal arm segments, USNM 6491; D, Same, distal arm segment, USNM E6302; E, Actinal view of distal arm segment, USNM E6302. *Ophiopaepale diplax*: F, Abactinal view of proximal arm segments, MCZ 5690; G, Actinal view of distal arm segment, MCZ 5458. Scale bar: A, C, F, 1 mm; B, D, E, G, 0.5 mm.

The next 2–3 segments rarely have more than a few scattered granules on the dorsal arm plate; granules often occur at the junction of the dorsal and lateral arm plates. Granulation does not extend farther on the arm. The first (undivided) ventral arm plate has a central naked region. The next 2–3 segments bear granules only at the junction of the distal piece of the ventral arm plate and the lateral arm plates; on the lateral and proximal regions of the lateral arm plates; and sometimes near the bases of the arm spines. The rest of the arm is naked actinally.

*Coloration.*—The color pattern of alcoholic and dried specimens is variable (Fig. 3D, E). Generally, the upper surface of the disc bears yellow-white spots on a darker, orange-yellow background. Large spots overlie the radial shields and marginal disc plates, and a dark crescent outlines the proximal edge of the unpaired interradial marginal plate. Other spots do not correspond to the locations of disc scales. The center of the disc frequently has a large irregular or subcircular spot. The spotted pattern continues onto the actinal interradial surface of the disc. The

oral frame and underside of the arm are uniformly pale yellow or yellow-white. The upper surface of the arm is banded. Band width is 1½–2 segments. Banding results from alternating dark and light background colors coinciding with regions of small and large light spots, respectively. The 2–4 distal pieces of each dorsal arm plate bear larger light-colored spots than other pieces. In many specimens, the pieces of the dorsal arm plate are outlined by the dark underlying intervertebral muscles, which show through the thin edges where pieces abut. Verrill (1899a) reported that Nutting's (1895) description of white spots on a brown disc is the color in life.

*Type-locality.*—Anguilla, Lesser Antilles, 180 fm.

*Distribution.*—Eastern Gulf of Mexico and throughout the Greater and Lesser Antilles; 56–211 fm (or as deep as 242 fm) on coral (Koehler 1914), "pentacrinus grounds" (Nutting 1895), and other coarse and hard substrata (Pierce and Patterson 1879). The bathymetric range of 38–250 fm given by Lyman (1883), Verrill (1899a, b), Meissner (1901), and Clark (1915) apparently includes a misidentified juvenile of *Ophiomusium* or *Ophiosphalma* from *Blake* sta 127 (38 fm) (MCZ 797). In addition to material examined by me, Clark (1921) reported *O. goesiana* from *Blake* sta 298 at 120 fm. Lyman (1883) and others reported it from *Blake* sta 101 at 175–250 fm, but the material (MCZ 252) has been lost.

*Remarks.*—Although Koehler (1904) examined and illustrated Ljungman's holotype, his fig. 3 showed entire dorsal arm plates. An earlier figure (Agassiz 1888) of non-type material showed fragmentation only for the first segment free of the disc. It is difficult to interpret from Nielsen's (1932) discussion if he examined Ljungman's holotype or relied on the published figures mentioned above to conclude that dorsal arm plates of *O. goesiana* are entire.

### *Ophiopaepale diplax* (Nielsen, 1932), new combination
Figs. 1B, 2B, 3F, 4D–E, 5F–G

*Schizoderma diplax* Nielsen, 1932:243 (listed), 335–339 (described), fig. 39.—Clark, 1940:343 (station data and material).—Fell, 1960:27 (listed).—Spencer & Wright, 1966:98 (listed).

*Material.*—PARATYPE (Universitetets Zoologiske Museum, Copenhagen): alcoholic specimen, dd 9.5 mm; Gulf of Panama, South of San José, Islas Perlas; Dr. Th. Mortensen's Pacific Expedition 1914–16, 27 Jan 1916, 25 fm.

Non-type material: (MCZ 5456), 5 dry spec., dd 8.1–15.9 mm; Gulf of California, Santa Inez Bay; Templeton Crocker Expedition, *Zaca,* sta 142-D-2/3/4, 11 Apr 1936, 30–50 fm.—(MCZ 5457), 3 dry spec., dd 7.8–15.6 mm; Gulf of California, Santa Inez Bay; Templeton Crocker Expedition, *Zaca,* sta 143-D-1, 13 Apr 1936, 20 (or 29?) fm.—(MCZ 5458), 3 dry spec., dd 7.6–11.0 mm; Gulf of California, Santa Inez Bay; Templeton Crocker Expedition, *Zaca,* sta 146-D-1, 17 Apr 1936, 35 fm.—(MCZ 5459), 3 dry spec., dd 5.8–13.8 mm; Gulf of California, Arena Bank; Templeton Crocker Expedition, *Zaca,* sta 136-D-1/14, Apr 1936, 45 fm.—(MCZ 5460), 5 dry spec., dd 6.6–9.7 mm; Lower California, Gorda Banks; Templeton Crocker Expedition, *Zaca,* sta 150-D-8/9, 22 Apr 1936, 40–60 fm.—(MCZ 5690), 1 dry spec., dd 6.0 mm; Colombia, Port Utria; University of Southern California, Hancock Pacific Expeditions, *Velero,* sta 856, 25 Feb 1938, 15–30 fm.—(MCZ 6172), 9 dry spec., dd 5.7–10.4 mm; Costa Rica,

14 mi SE of Judas Pt.; N.Y. Zoological Society, Department of Tropical Research, Eastern Pacific *Zaca* Expedition 1937–38, sta 214-D-1/2/3/4, 1 Mar 1938, 9°19′32″N, 84°29′30″W to 9°17′40″N, 84°27′30″W, 42–61 fm, 4-ft *Blake* dredge.— (MCZ 6173), 10 alcoholic spec., dd 6.9–10.6 mm; same data as MCZ 6172.

*Diagnosis.*—1 plate at margin of disc in each interradius; longer than wide. Genital slits extending onto abactinal surface of disc; bordered by flattened, square papillae on large accessory scales. Oral shields triangular, naked; adoral shields naked. Arm length 4–7 times disc diameter. Dorsal arm plates greatly fragmented; distal border composed of 2 large lateral and 1 small central pieces. Distal tentacle scales lamelliform.

*Remarks.*—The description of *O. goesiana* given above generally fits *O. diplax.* The notes given below emphasize major differences, and Nielsen's (1932) thorough description is modified based on examination of new material collected outside the type-locality.

In non-type material and one paratype, no distinct band of larger granules borders the disc; granules increase gradually in size from center to margin as in *O. goesiana* rather than abruptly as Nielsen (1932) described. Radial shields of adjacent radii extend well beneath a single interradial plate and nearly meet at the midline (Fig. 3F); the interradial plate is longer than wide (i.e., with a short side along the disc margin). On most specimens, granules cover the bottom edge of the dental plate and border the sutures of the oral frame; but the centers of the oral and adoral shields and, contrary to Nielsen (1932), oral plates are naked; the oral plates are granulated only in some larger specimens. Spination of the dental and oral plates and adoral shields is the same morphologically and meristically as in *O. goesiana* except that the 2 distalmost oral papillae of *O. diplax* are shorter (Fig. 4D). The paired oral plates are more extensively in contact; the adoral shields are wider and more tapering (i.e., proximal and distal margins divergent); oral shields are triangular, with proximal sides in some specimens concave. Genital slits appear to extend onto the abactinal surface of the disc because of the greater protrusion of the distal genital scale and of specialized scales on the genital bar at the distal end of the slit (Fig. 4E); flattened, square papillae border the distal ⅓–½ of the margin of the slit (Nielsen 1932, fig. 39c). Arm length is 4–7 times the disc diameter. The arm is widest at segment 3–4, sometimes 5; this might reflect the relatively shorter arm length and shorter proximal vertebrae (Fig. 2B) compared to *O. goesiana*; i.e., a greater number of segments lie beneath the disc. Dorsal arm plates are more greatly fragmented (20–25 pieces; Nielsen 1932) and are bordered distally by 2 large lateral pieces and 1 small, keystone-like central piece (Fig. 5F; cf, Nielsen 1932, fig. 39c). The distal pieces of the ventral arm plates are proportionately wider than those of *O. goesiana.* The number of arm spines is more variable, generally 3–4 on proximal segments free of the disc (not regularly 4 as found by Nielsen 1932); distally, 4 arm spines are usually found. A fourth, uppermost arm spine, if present, is short; no arm spine exceeds ½ the length of a segment. Tentacle scales are proportionately larger than those of *O. goesiana,* and those on free segments of the arm do not become progressively spiniform (Fig. 5G). Coloration is similar to that of *O. goesiana,* but the banding extends onto the ventral arm plates in the distal half of the arm; a small central white spot occurs on the disc of many specimens, and a distinct white spot occurs abactinally on the arms every few segments. *Ophiopaepale diplax* ranges from

Santa Inez Bay, Gulf of California, to Port Utria, Colombia, in 25–61 fm and may occur as shallow as 15 fm. It was taken on mud, shell, and rock by the *Zaca* (Beebe 1938; Clark 1940).

*Discussion.*—*Ophiopaepale* was included in the same family or subfamily with *Ophioderma* and separated from *Ophiura* (=*Ophioglypha*) and *Ophiolepis* by early workers (Ljungman 1872; Verrill 1899a, b). It was later removed from association with *Ophioderma* and placed with *Ophiura* and *Ophiolepis* (Bather *et al.* 1900; Meissner 1901; Delage and Hérouard 1903; Koehler 1907), but Koehler (1914) returned it to the Ophiodermatidae. Matsumoto (1915) separated *Ophiopaepale* from the other three genera entirely, placing it in his new family Ophioleucidae; his treatment was accepted by H. L. Clark (1915, 1941) and A. H. Clark (1921, 1954). Nielsen (1932) assigned his new genus *Schizoderma* to the Ophiodermatidae but stated his willingness to assign it with *Ophiopaepale* to the Ophioleucidae. Most recently, Fell (1960) and Spencer and Wright (1966) treated *Ophiopaepale* and *Schizoderma* as ophiodermatids, not ophioleucids or ophiurids; and Madsen (1983) excluded *Ophiopaepale* from the Ophioleucinae, which he assigned to the Ophiuridae. Familial assignment of these genera was unspecified in other works cited in the synonymies given above for *Ophiopaepale* and *O. goesiana.*

The differences in systematic treatment have largely been due to the authors' interpretations of the morphology and spination of the arms, structural relationship of the arms to the disc, and spination of the oral frame. *Ophiopaepale* is retained in the Ophiodermatidae in the present work. Although the arms are long and slender, they are widest basally, at segments 3–5. Arm spines are few (3–4), but some other ophiodermatids also have relatively few arm spines (Fell 1960). The arms are inserted laterally into the disc, as in ophiodermatids; the appearance of a ventral, less firm insertion is only due to the elongated and upturned genital slits. The disc is almost fully granulated; the granules are tables (morphologically similar to those of some aspidochirote holothuroids) rather than rounded granules of some *Ophioderma* species, but no other comparative evidence of granule morphology is available on which to base a conclusion. Spination of the oral frame is identical to that of *Ophioderma.* Reliance on the number of infradental papillae alone is presently unwarranted for familial assignment because the nature of infradental papillae often has been misinterpreted; moreover, previous authors have not agreed on the number (indeed, the presence) of infradental papillae in ophiodermatid brittle stars. Madsen's (1983) inclusion of the closely related Ophioleucidae as a subfamily of Ophiuridae complicates assignment of *Ophiopaepale.* Re-examination of disc granulation, oral armature, and other features in families of the Chilophiurina would be well advised.

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